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Sense organs in antennae of *Jaliscoa hunteri* (Hymenoptera Pteromalidae)

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Abstract

Parasitoid antennae play fundamental roles in the host acceptance and location processes. The functions of antennal sensory organs can be inferred based on their types, quantities, and distributions. The objective of this study was to describe the external sensilla present in the antennae of male and female *Jaliscoa hunteri* (Crawford) (Hymenoptera Pteromalidae), an ectoparasitoid of species of Curculionidae and Bruchidae (Coleoptera), using electron scanning microscopy. Seven morphological types of sensilla were found on antennae of both males and females: four poreless trichoid sensilla (ST1-AP to ST4-AP), one multipored plate sensillum (MPS), one unipored chaotic sensillum (ChS-UP), and one basiconic capitate sensillum (BCS). We recorded the abundance and distribution of these sensilla types on antennae of both sexes. Overall, we found differences in abundances of ST1-AP, ST2-AP, ST3-AP, MPS and ChS-UP sensilla, as well as in distribution and abundance of BCS sensilla between males and females, indicating sexual dimorphism in the antennae of *J. hunteri*. Based on their presence, abundance and distribution, and following available, published information, we discussed some plausible functions of the antennal sensilla of *J. hunteri*, such as perception of vibrations (mechanoreception) and odors (chemoreception).

Key words: parasitoid, host location, host acceptance, antennal sensilla, cryptic host, Curculionidae, Bruchidae.

Introduction

Reproductive success in parasitoids depends on a series of events that involve host location at long and short distances and host assessment for offspring development, among other processes (Vinson, 1997). During these processes, females use different stimuli, or signals, that lead gradually to host acceptance or rejection (Vinson, 1976; 1981). Detection and discrimination of key environmental stimuli relies mainly on sensory organs called sensilla, which can be distributed in different parts of the organism, such as antennae, ovipositor and tarsus (Chapman, 1998).

In most parasitoid species, the precise mechanisms involved in the host searching and acceptance processes are still unknown. However, through descriptive study of antennal sensilla it is possible to infer on important aspects of the roles of antennae in those processes. Antennal sensilla may have different sensorial functions, such as touch (mechanical sensillum), and smell and taste (chemical sensillum) (Schneider, 1964; Zacharuk, 1985; Chapman, 1998), which help parasitoid females locate, recognize, and accept or reject hosts, or habitats (Isidoro *et al.*, 1996; 2001; Vinson, 1997). Exploratory study of sense organs can help to understand the behaviours of parasitoids of cryptic hosts, i.e., those developing inside fruits, seeds and stems (Hanson and Gauld, 2006). Additionally, exploratory studies may also lead to more efficient mass rearing of parasitoids for use in biological control.

Jaliscoa hunteri (Crawford) (Hymenoptera Pteromalidae) is a solitary ectoparasitoid of at least 17 species of Curculionidae and two species of Bruchidae (Cross and Mitchell, 1969; Cross and Chesnut, 1971). It is reported as a biological control agent of the pepper weevil *Anthonomus eugenii* (Cano) (Coleoptera Curculionidae) (Rodriguez-Leyva *et al.*, 2000; Schuster, 2007), the major pest of peppers in the USA, Mexico and Central America (Riley and Schuster, 1992; Rodríguez-Leyva *et al.*, 2007). This pest was recently detected in the Netherlands and Italy, though it was soon eradicated (EPPO, 2011; Speranza *et al.*, 2014). Although there is an interest in the study of this parasitoid for biological control of pepper weevil, the mechanisms by which it locates and accepts its cryptic hosts (e.g., Bruchidae larvae in seeds and *A. eugenii* in pepper fruits) are unknown. It is assumed that *J. hunteri* uses a variety of physical, chemical and mechanical signals from its hosts or its hosts' habitat, as known for other parasitoids (Mbata *et al.*, 2005; van Baaren *et al.*, 2007). However, there is no basic information on the sensory organs of this species to support this assumption. Thus, the objective of this study was to describe the morphology, location, abundance and distribution of the sensory organs present on the antennae of *J. hunteri* male and female.

Materials and methods

Insects

Adult *J. hunteri* were reared on chickpea weevil larvae, *Callosobruchus maculatus* (F.) (Coleoptera Bruchidae), in the biological control laboratory at the Colegio de Postgraduados, Texcoco, State of Mexico. Both species were kept in a bioclimatic chamber (25 ± 2 °C, 60-70% R.H., 12:12 L:D), following the methodology described by Rodríguez-Leyva *et al*., (2002) and Vasquez *et al*.,

(2005). Briefly, the method consists of offering chickpeas infested by last-instar weevil larvae parasitoid females.

Sample preparation

A group of 50 adult *J. hunteri* (females and males) less than 12 h old were sacrificed in 70% ethanol to excise their antennae. Dissections were performed with entomological forceps No. 5 (Fisher Scientific) under a stereoscopic microscope at 20× magnification (VELAB®, Model VE-S4, Madrid, Spain). Antennae were placed separately (male and female) in 70% ethanol for 24 hours, after which they were dehydrated in a series of alcohol solutions: 75, 80, 90% and absolute alcohol, one hour per solution.

The dehydrated antennae were transferred to a critical point drier (Samdri-780A®, TOUSIMIS Research Corporation, Rockville, USA) for 45 min. One antenna of each pair was mounted dorsally and the other ventrally on a copper sample holder. For mounting, carbon adhesive tape was used, and antennae were coated with gold-palladium (40:60) in a JEOL® ionizer (JFC-1100, Tokyo, Japan) for 10 min for observation in an electron microscope.

Scanning electron microscopy (SEM)

External antennal morphology was examined in a scanning electron microscope (JEOL-JSM6390, Tokyo, Japan) in the electron microscopy laboratory at the Colegio de Postgraduados, Texcoco, State of Mexico. Micrographs were made of male and female antennae, as well as of the different sensilla present on them.

Sensilla description, identification and measurement

The antennal sensilla of male and female *J. hunteri* captured in the micrographs were described per the terminology, classification and identification of Chapman (1982; 1998) and Onagbola and Fadamiro (2008). Sensilla were identified on the basis of presence, absence, and position of pores. Measurement of total length, base width, and diameter of the insertion well (when present) of each sensilla type was expressed in micrometers (μm) with the software Image-Tool for Windows, Version 3.0 (Wilcox *et al*., 2002).

Statistical analysis

The sensilla present on the dorsal and ventral surfaces of the antennae of both sexes were counted and measured. Abundance and distribution of the different sensilla types was observed on 12 antennae of each sex, while mean dimensions (mean μm ± S.E.) were estimated from images of 30 individual sensilla of each type per sex. Comparisons between sexes were made with Student *t* tests (Statistix 8, Version 8.1, 2005), to determine any significant sexual differences ($P < 0.05$).

Results

General morphology of the antennae

The antennae of the parasitoid *J. hunteri* are geniculate in both sexes, but they differ significantly in length: females (1295.6 ± 15.6 μm) have longer antennae than males (1146.9 ± 22.1 μm) ($t = 5.35$, $P < 0.001$). The antenna has four areas: the radicle, scape, pedicel and flagellum (figure 1A). The radicle (Rd) was measured separately from the scape and makes up approximately 3% of the total length of the antenna, with average values of 34.4 ± 1.4 μm (mean ± S.E.) for males and 43.7 ± 1.3 μm for females. The scape (Sc) is cylindrical, approximately six times longer than wide (length 304.2 ± 4.2 μm in males, and 371.8 ± 6.5 μm in females), and accounts for approximately 28% of the length of the antenna. The pedicel (Pd) is short and barrel-shaped, 75.4 ± 2.4 μm long in males, and 97.7 ± 2.3 μm in females; it is ~7% of the length of the antenna. The flagellum (Fl) constitutes approximately 62% of the total antenna length and has three parts: a basal part of two annuli (An1 and An2), which are approximately three times wider than long. The intermediate part, the funicle, has six cylindrical antennomeres (Fn1 to Fn6). The distal segment, called the spike, has three antennomeres (Cl1, Cl2 and Cl3), which are flat and stretched to form a point (figure 1A). The flagellum in males has a total length of 735.4 ± 11.9 μm and in females 782.4 ± 14.1 μm.

Types of antenna sensilla

Under a stereoscopic microscope, the surface of *J. hunteri* antennae of the two sexes seems to be similar. However, the abundance and distribution of the sensilla differ (figure 1B, 1C, 1D and 1E). *J. hunteri* antennae (of males and females) have seven morphological types of sensilla: four types of poreless trichoid sensilla (ST1-AP, ST2-AP, ST3-AP and ST4-AP), one multiporous plate sensillum (MPS), one unipore chaetic sensillum (ChS-UP), and one pacifier-shaped, basiconic, capitate sensillum (BCS). Distribution of sensilla types on each segment of the female and male antennae is shown in table 1.

Poreless type 1 sensilla trichoid (ST1-AP)

These are found inserted in a small conical base from which a thin solid axis emerges and bends strongly at the apex. They are located only at the distal tip of the last antennomere of the spike in antennae of both sexes (figure 2A). The size of this type of sensilla varied from 11.8 ± 0.11 μm to 11.09 ± 0.21 μm long, and 1.01 ± 0.01 μm to 0.92 ± 0.02 μm wide at the base. Female antennae have a greater number of this type of sensilla compared to males (table 1D).

Poreless type 2 sensilla trichoid (ST2-AP)

These sensilla are long conical structures that end in a straight pointed apex. The surface along their axes has longitudinal lines. This type of sensilla are found inserted profusely in alveoli of the antennal cuticle (figure 2B). They are widely distributed in the pedicel (table 1A), annuli (table 1B), funicle (table 1C), and spike (table 1D) of both sexes. However, there are fewer on female compared to male antennae ($t = 20.6$, $P < 0.01$). Average length is 20.13 ± 0.41 μm and width at the base is 1.61 ± 0.03 μm.

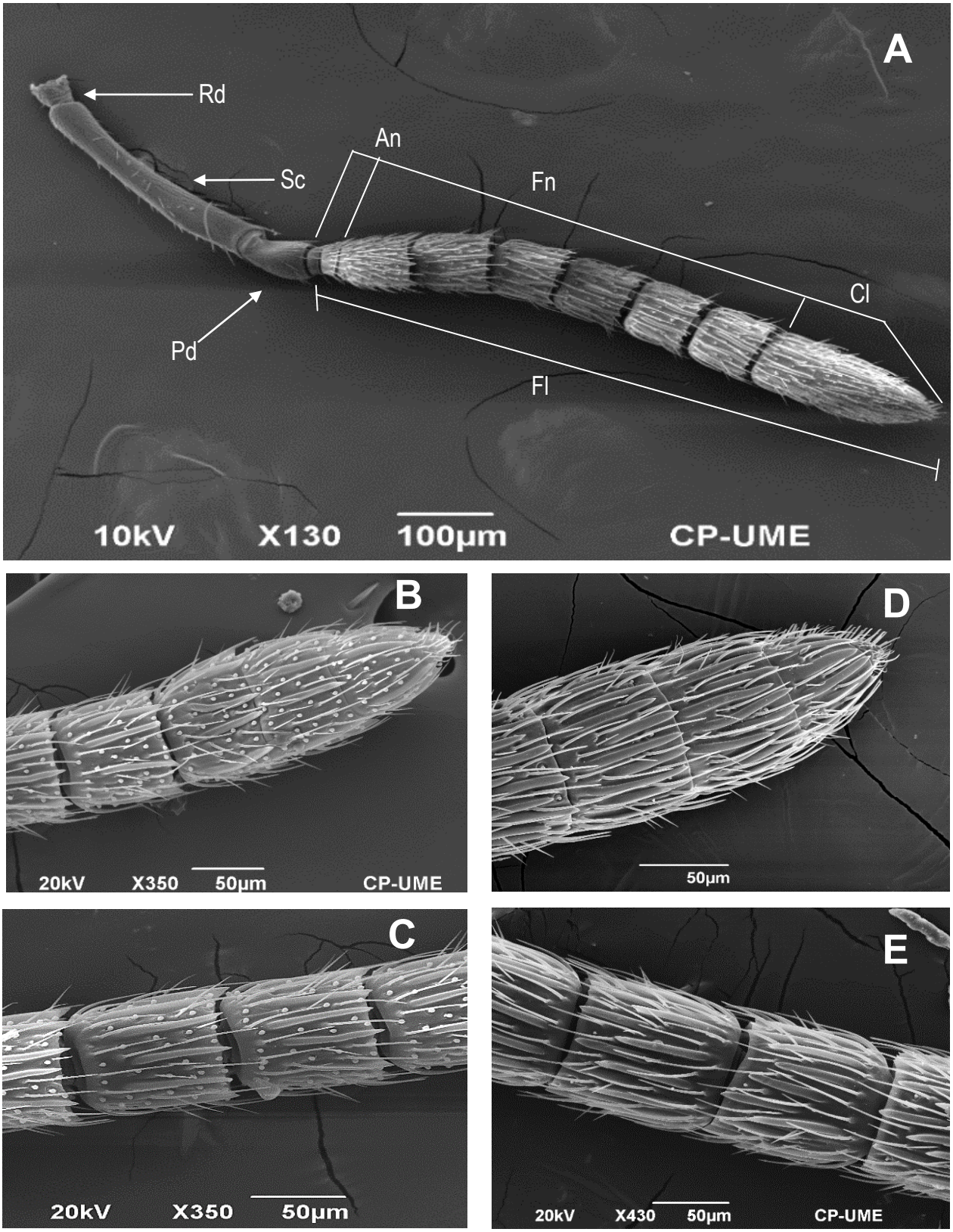

Figure 1. *J. hunteri* antennae. **A)** Geniculate antenna of male comprising a radicle (Rd), scape (Sc), pedicel (Pd) and flagellum (Fl) with two annuli (An), one funicle (Fn), with six antennomeres and a spike (Cl); **B)** Male antennal spike; **C)** Male antennal flagellum; **D)** Female antennal spike; **E)** Female antennal flagellum.

Table 1. Abundance and distribution of different antennal sensilla on female and male *J. hunteri*.

	Sensilla	Sex	Radicle	Scape	Pedicel	Total	
A	ST2-AP	Male	—	78 ± 3.5	26 ± 1.2	104 ± 3.9	**
		Female	—	101 ± 4.5	33 ± 4.7	134 ± 6.4	
	ST4-AP	Male	17 ± 1.1	—	3 ± 0.2	20 ± 1.2	
		Female	17 ± 1.1	—	3 ± 0.9	20 ± 1.2	

	Sensilla	Sex	Annulus segment		Total	
			An1	An2		
B	ST2-AP	Male	10 ± 0.6	19.2 ± 1.4	29 ± 1.4	**
		Female	8 ± 0.4	17.9 ± 1.1	26 ± 0.82	

	Sensilla	Sex	Funicle segments						Total	
			Fn1	Fn2	Fn3	Fn4	Fn5	Fn6		
C	ST2-AP	Male	54 ± 2.4	22 ± 0.9	22 ± 0.9	21 ± 0.9	20 ± 1.1	18 ± 0.5	156 ± 4.0	**
		Female	36 ± 0.6	23 ± 0.7	18 ± 0.7	20 ± 1.1	18 ± 0.4	17 ± 0.5	132 ± 2.2	
	ST3-AP	Male	—	35 ± 0.7	35 ± 1.9	38 ± 0.1	34 ± 1.7	41 ± 1.0	271 ± 3.7	**
		Female	20 ± 0.8	46 ± 0.7	46 ± 0.8	47 ± 1.1	43 ± 0.1	47 ± 0.9	248 ± 2.7	
	MPS	Male	11 ± 0.4	13 ± 0.4	13 ± 0.3	13 ± 0.4	14 ± 0.2	14 ± 0.4	108 ± 1.3	**
		Female	15 ± 0.6	20 ± 0.4	20 ± 0.4	22 ± 1.2	20 ± 0.3	20 ± 1.4	117 ± 2.1	
	BCS	Male	72 ± 1.8	82 ± 1.5	81 ± 1.7	75 ± 3.2	76 ± 3.2	79± 2.6	465 ± 6.1	**
		Female	2.6 ± 0.2	4 ± 0.2	4 ± 0.3	4 ± 0.2	4 ± 0.3	2 ± 0.3	20 ± 0.6	

	Sensilla	Sex	Segments of the spike			Total	
			Cl1	Cl2	Cl3		
D	ST1-AP	Male	—	—	—	20 ± 0.4	**
		Female	—	—	—	40 ± 1.9	
	ST2-AP	Male	18 ± 0.6	16 ± 0.8	17 ± 0.7	50 ± 1.4	**
		Female	20 ± 0.9	20 ± 0.4	5 ± 0.6	45 ± 1.4	
	ST3-AP	Male	35 ± 0.9	31 ± 0.8	21 ± 1.3	88 ± 2.4	**
		Female	43 ± 1.3	39 ± 1.9	17 ± 0.3	99 ± 2.1	
	MPS	Male	12 ± 0.2	12 ± 0.4	7 ± 0.3	31 ± 0.6	**
		Female	19 ± 0.8	18 ± 0.6	11 ± 0.4	49 ± 1.1	
	ChS-UP	Male	—	—	—	20 ± 0.5	**
		Female	—	—	—	34 ± 1.1	
	BCS	Male	62 ± 3.1	71 ± 2.4	51 ± 1.4	184 ± 5.2	**
		Female	3 ± 0.2	2 ± 0.2	1 ± 0.2	6 ± 0.3	

Mean ± SE of number of sensilla in each antenna segment (n = 12 individuals per sex). ST1-AP: poreless type 1 sensilla trichoid; ST2-AP: poreless type 2 sensilla trichoid; ST3-AP: poreless type 3 sensilla trichoid; ST4-AP: poreless type 4 sensilla trichoid; MPS: multipore plate sensilla; ChS-UP: unipor chaetic sensilla; BCS: basiconic capitate sensilla. **indicates that the total number of each type of sensilla are statistically different between males and females (*t* test, $P \leq 0.05$).

Poreless type 3 sensilla trichoid (ST3-AP)

These sensilla are long, needle-like structures that emerge from the antennal cuticle with a curved base (no insertion is observed) and smooth cuticle (figure 2C). They are found in the antennomeres of the funicle and spike of both sexes, except for Fn2 in males (table 1C). The mean length of this type of sensilla is 41.05 ± 0.44 µm and mean width is 2.69 ± 0.05 µm. They are more abundant in female than in male antennae (t = 13.86, $P < 0.01$).

Poreless type 4 sensilla trichoid (ST4-AP)

These sensilla are short, conical structures with a smooth surface that ends in a blunt apex. They are inserted in deep wells (4.32 ± 0.12 µm in diameter), exclusively on the basal part of the radicle and pedicel (figure 2D) in groups of two to five. They measure 8.23 ± 0.39 µm long and 1.38 ± 0.02 µm at the base.

Multiporous plate sensilla (MPS)

Multiporous plate sensilla emerge from the cuticle, rising parallel to the antennal axis. They are long, sausage shaped plates ending in a blunt tip, with multiple pores on the surface (figure 2B). MPS sensilla are on the antennomere Fn1 of the Cl3 funicle of the spike, located between sensilla ST2-AP and ST3-AP, and distributed in rings on the antennomeres. MPS sensilla are 55.20 ± 0.67 µm long by 5.28 ± 0.09 µm wide. These sensilla are more abundant on female compared to males antennae (t = 21.9, $P < 0.01$).

Unipore chaetic sensilla (ChS-UP)

These are inserted in a narrow conical base from which they project perpendicular to the antenna axis. Their surface is rutted and they end in a blunt point with an apical pore (figure 2E). This type of sensillum is 10.86 ± 0.13 µm long by 1.40 ± 0.02 µm wide at the base. Unipore chaetic sensilla are found only at the distal end of the

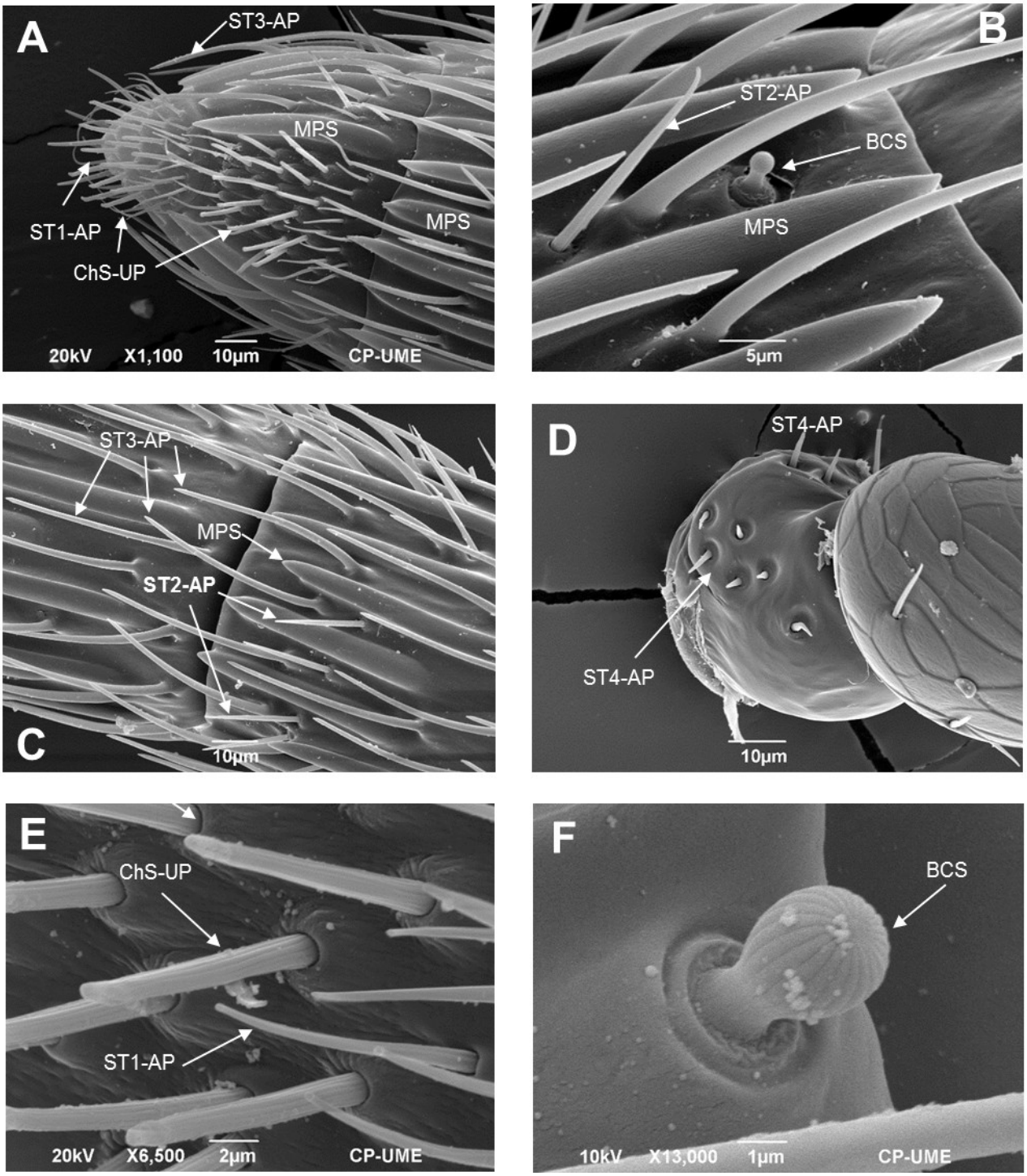

Figure 2. Type, location and morphology of sensilla on *J. hunteri*. **A)** Last segment of the spike showing the location of poreless type 1trichoid sensilla (ST1-AP) and unipore chaetic sensilla (ChS-UP) female antenna; **B)** Funicle segment of the antenna of a female; location of the poroless type 2 sensilla trichoid (ST2-AP), multipore plate sensilla (MPS) and basiconic capitate sensilla (BCS) located on the distal part of the funicle; **C)** Location and morphology of poreless type 3 sensilla trichoid (ST3-AP), poreless type 2 sensilla trichoid (ST2-AP) and multiporous plate sensilla (MPS) female antenna; **D)** Location of poreless type 4 sensilla trichoid (ST4-AP) on the antenna radicle female antenna; **E)** Morphology of the ChS-UP that exhibit longitudinal ornamentations on the axis and pore on the apex female antenna; **F)** Morphology of BCS with ornamentations on the bulb male antenna.

ventral part of antennomere Cl3 of the spike in both sexes (figure 2A), and in greater numbers on female compared to male antennae ($t = 11.50$, $P < 0.001$).

Basiconic capitate sensilla (BCS)

These sensilla are bulb-shaped (2.28 ± 0.06 µm in diameter). They have a slotted surface, similar to orange fruit segments (figure 2F). The bulb emerges from a stem 1.39 ± 0.02 µm long by 1.50 ± 0.02 µm wide at the base, which is immersed in a rough shallow cuticular depression (2.74 ± 0.02 µm diameter). BCS are found on all the antennomeres of the antennal flagellum in males, where they are found in greater numbers along the antennomeres, from Fn1 to Cl3 (table 1C and 1D). On the female antenna, these sensilla are confined to the ventral and distal portions of antennomeres (figure 1B).

Abundance and distribution of antenna sensilla

Each type of antennal sensillum possesses a specific number, location and distribution pattern on the antennae of *J. hunteri* males and females. The main differences between sexes are observed in the abundance and distribution of the different sensilla type on the antenna flagellum, (table 1B, 1C and 1D).

ST1-AP are located only on antennomere Cl3 of the spike, specifically on the antennomere apex in both sexes and on the ventral part of the antennomere in females (figure 2A). The ST1-AP are more abundant on antennae of females ($t = 10.47$, $P < 0.001$) compared to males (table 1D). Likewise, the ChS-UP antenna sensilla are distributed on the tip and ventral part of the Cl3 antennomere of the spike where they are grouped and surrounded by ST1-AP sensilla (figure 2A). The abundances of ChS-UP sensilla differ between male and female antennae ($t = 11.50$, $P < 0.001$), with ca. twice as many sensilla in females compared to males (table 1D). In contrast, the ST2-AP sensilla are more abundant on male antennae ($t = 20.68$, $P < 0.001$), and are distributed on the scape segments, the pedicel (table 1A) and flagellum (of antennomere An1 of the anulli to antennomere Cl3 of the spike) of both sexes (table 1C and 1D).

ST3-AP sensilla are found on male antennae from the funicular antennomere Fn2 to Cl3 of the spike, while in female antennae they appear from antennomere Fn1 of the funicle to antennomere Cl3 of the spike (table 1C and 1D); ST3-AP abundance is greater in females ($t = 13.96$, $P < 0.001$). The distribution of ST4-AP is limited to the radicle and ventral surface of the pedicel, in the articulation of the elbow where it is attached to the scape (table 1A). These sensilla have similar distributions, locations, and abundances in the two sexes.

MPS sensilla are distributed in rings that surround the antennomeres and can be observed from antennomere Fn1 to the last Cl3 antennomere of the spike in both sexes, but their number is lower in male than in female antennae ($t = 21.92$, $P < 0.001$). In female antennae, the MPS form double rings on the antennomeres (figure 1E). The bulb-shaped basiconic capitate sensilla (BCS) differ between males and females in their distributions and abundances (table 1C and 1D), and are significantly more abundant in male than in females ($t = 63.62$, $P < 0.001$).

Overall, the differences in abundances of ST1-AP, ST2-AP, ST3-AP, MPS and ChS-UP sensilla, as well as in distribution and abundance of BCS sensilla between males and females indicate sexual dimorphism in the antennae of the parasitoid *J. hunteri*.

Discussion

Seven types of morphologically different sensilla were found in antennae of both sexes of *J. hunteri*. Of these sensilla, four were poreless trichoid types (ST1, ST2, ST3 and ST4-AP). ST2-AP and ST3-AP were the most abundant and widely distributed over the antennae, while ST1-AP and ST4-AP were the least abundant. ST1-AP sensilla were located on antennomere Cl3 of the spike, while ST4-AP were present on the radicle and scape. In addition to these trichoid sensilla, multiporous plate sensilla (MPS), one pacifier-shaped basiconic capitate sensilla and one unipore chaetic sensilla (ChS-UP) were identified.

J. hunteri is a known generalist parasitoid of cryptic species (Hansson and Gould, 2006). The different types of sensilla present on their antennae suggest that the females can use mechanical (vibrations) and olfactory (semiochemical) signals to locate their hosts hidden in vegetative structures or seeds, as described for other species (Onagbola and Fadamiro, 2008). The sensilla found on *J. hunteri* antennae may be categorized as follows, based on our observations and prior studies (Wibel *et al*., 1984; Pettersson *et al*., 2001; van Baaren *et al*., 2007; Onagbola and Fadamiro, 2008), 1) Mechanoreceptors: sensilla ST1-AP and ST2-AP; 2) Proprioreceptor: ST4-AP; 3) Chemoreceptors: ST3-AP, MPS, ChS-UP; 4) Thermo-hygro-receptor: BCS.

Mechanoreceptor sensilla

Chapman (1998) described these sensilla as poreless trichoid organs, which are found inserted in conical bases of the antennal cuticle and may have longitudinal ornamentations. In most species of Hymenoptera, these sensilla are numerous and distributed along the antenna covering the entire surface. When the antenna encounters a substrate, the sensilla move within their conical base, indicating to the female that she is touching a substrate (van Baaren *et al*., 2007). Based on the characteristics described by Chapman (1998), the trichoid sensilla ST1-AP and ST2-AP found on *J. hunteri* are mechanoreceptors.

Sensilla ST2-AP on *J. hunteri* described in this study is very similar to the "poreless trichoid B" sensilla described on antennae of *Trichogramma nubilale* Ertle et Davis (Olson and Andow, 1993) and to the tactile sensilla denominated "mechanoreceptor hairs" in the parasitoid *Rhopalicus tutela* (Walker) (Pettersson *et al*., 2001), possibly corroborating the mechanoreceptor function in *J. hunteri*.

ST1-AP sensilla, like ST2-AP sensilla, found in this study have been described on other species of Hymenoptera from various families, for which a mechanoreceptor function has been reported for both types (Olson and Andow, 1993; Isidoro *et al*., 1996; van Baaren *et*

al., 1996; 1999; Amornsak *et al*., 1998; Pettersson *et al*., 2001; Roux *et al*., 2005). Isidoro *et al.* (1996) suggested that poreless trichoid sensilla may be involved in locating and discriminating cryptic hosts. Several parasitoid species examine their hosts and the plant structure where they develop by tapping with the ventro-apical part of the antenna mace. For this reason, it is probable that the ST1-AP sensilla described in this study function as mechanoreceptors. The tapping behaviour has been observed in *J. hunteri* on the chickpeas where the alternative, laboratory host was located (Gómez-Domínguez, personal observation).

Proprioreceptor sensilla

The sensilla denominated proprioreceptors (= proprioceptor) are those that are located in the unions between segments, or sclerites, whose function is to sense movement of a cuticular element with respect to another (Chapman, 1998). The ST4-AP sensilla described in this study for *J. hunteri* are poreless trichoid sensilla, which are found only on the radicle and articulation of the pedicel elbow, as described by Chapman (1998). They are morphologically similar to those described on antennae of parasitoids such as *Gryon boselli* Mineo et Szabo (Villa and Mineo, 1990) and *Trichogramma australicum* Girault (Schmidt and Smith, 1987; Amornsak *et al*., 1998). The cited studies indicate a proprioreceptor function, and thus the ST4-AP sensilla of *J. hunteri* may have the same function.

Chemoreceptor sensilla

The chemoreceptors (olfactory and gustative) perceive volatile and non-volatile chemical substances. These sensilla have tubular bodies with innervation of numerous internal dendrites (Chapman, 1998). The olfactory chemoreceptor sensilla perceive volatile chemical substances and morphologically have a smooth surface with fine ornamentations or numerous pores on the entire surface (van Baaren *et al*., 2007). Based on the above, it is likely that ST3-AP and MPS sensilla have an olfactory-type chemoreceptor function.

ST3-AP sensilla have been reported in several parasitoid species, denominated “multiporous trichoid sensilla with pores in the wall” (Wibel *et al*., 1984; Pettersson *et al*., 2001; Bleeker *et al*., 2004). However, pores were not observed in the wall of these sensilla in our study. ST3-AP morphology in our study is similar to the chemoreceptors of the thin wall described on the antennae of *Nasonia vitripennis* (Walker) (Wibel *et al*., 1984), “sensilla trichoidea" in *R. tutela*, (Pettersson *et al*., 2001) and “sensilla trichoidea C” in *T. nubilale* (Olson and Andow, 1993). Electrophysiological studies have confirmed the function of sensilla morphologically equal to those described in our study as receptors of sexual pheromones in *Neodiprion sertifer* Geoffroy (Hymenoptera Diprionidae) (Hansson *et al*., 1991). In *J. hunteri*, the greater abundance of ST3-AP sensilla observed in male antennae than in female antennae may likewise be related to detection of the female sex pheromones by males.

Plate sensilla are considered olfactory chemoreceptors. These are found in both males and females, distributed around the antennomeres of the flagellum (Chapman, 1982). The multiporous sensilla (MPS) described in our study is reported as widely distributed sensilla on antennae of parasitic wasps (Barlin and Vinson, 1981; Wibel *et al*., 1984; Olson and Andow, 1993; Amornsak *et al*., 1998; Pettersson, 2001). The multiple pores suggest an olfactory function (Barlin and Vinson 1981; Ochieng *et al*., 2000; Bleeker *et al*., 2004; Roux *et al*., 2005). The greater abundance of these sensilla in *J. hunteri* females contrasts with reports for females of other species of Hymenoptera (Navasaro and Elzen, 1991; van Baaren *et al*., 1999; Ochieng *et al*., 2000; Bleeker *et al*., 2004). However, their position and distribution could indicate a function as detectors of semiochemicals associated with the host’s habitat (Bleeker *et al.*, 2004), as occurs in other parasitoids of cryptic species, such as *Pteromalus cerealellae* (Ashmead) (Onagbola, 2008).

Gustatory chemoreceptors perceive non-volatile chemical substances. Van Baaren *et al*. (2007) point out that these sensilla are more abundant in females than in males. Their surface is rutted longitudinally and have one terminal or sub-terminal pore. The axis of this sensillum is generally inserted in a mobile conical base, indicating that in most cases the gustatory function is associated with a tactile function (mechanical) since it is necessary to touch the substrate to be in contact with non-volatile chemical substances. The unipore chaetic sensilla (ChS-UP) described for *J. hunteri* in our study are morphologically similar to gustatory chemoreceptors, as described above. Moreover, their morphology and location are similar to those of sensilla described in other insects, such as the “thick-walled chemoreceptors” of *N. vitripennis* (Slifer, 1969; Wibel *et al*., 1984), “trichoid D sensilla” in *T. nubilale* (Olson and Andow, 1993), “unipore gustatory sensilla” on antennae of parasitic wasps (Isidoro *et al*., 1996), and “basiconic sensilla in F” in Braconidae, including *Cardiochiles nigriceps* Vireck (Norton and Vinson, 1974). ChS-UP sensilla may be categorized as contact chemoreceptors, given the presence of a terminal pore, their rutted surface, and position with respect to the antennal axis, (Altner and Prillinger, 1980; Olson and Andow, 1993; Isidoro *et al*., 1996; Pettersson *et al*., 2001). In general, ChS-UP sensilla are confined to the apices of *J. hunteri* antennae, making them the first sensilla to contact substrates, as observed in other species of Pteromalidae, e.g., *P. cerealellae* (van Baaren *et al*., 2007). Thus, their location suggests a role as contact chemoreceptors (Wibel *et al*., 1984, Pettersson *et al*., 2001) involved in recognizing and accepting hosts (Borden *et al*., 1973).

Thermo-hygro-receptors

Thermo-hygro receptive sensilla are rare, present on the antennomeres of some parasitoid species, and generally protected or inserted in small surface depressions of the cuticle (Altner and Linde, 1980; van Breen *et al*., 2007). Basiconic capitate sensilla (BCS) are bulb-shaped; in this study, they were distributed in greater numbers along and both dorsally and ventrally the antennomere of the flagellum. Their morphology is similar to that of the thermo-hygroreceptors described above,

the "sensilla in multiporous pegs" of pteromalids (Barlin *et al*., 1981), as well as in other parasitoids where they are denominated "basiconic capitate peg" in *N. vitripennis* (Wibel *et al*., 1984), or "Sensilla coeloconic type I" on antennae of *Cotesia* spp. (Bleeker *et al*., 2004).

Van Baaren *et al*. (1996) and Olson and Andow (1993) mention the presence of pores in the furrows of the bulbous tip of the BCS sensilla, which suggest an olfactory function (Wibel *et al*., 1984; Pettersson *et al*., 2001). Pores indicating a chemoreceptor function were not observed, however, on the bulbous tip of *J. hunteri* BCS. These sensilla are morphologically more similar to the sensilla found on other arthropods, which suggests a thermo-hygroreceptor function (Altner *et al*., 1983; Wibel *et al*., 1984).

Conclusion

In general, the morphology, abundance and distribution of the trichoid sensilla ST1-AP, ST2-AP and ST4-AP suggest that they function as mechanoreceptors on the antennae of *J. hunteri* males and females. On the other hand, the sensilla ST3-AP, MPS and ChS-UP are most likely involved in the reception of olfactory chemical and contact signals from the host or its habitat, implying that chemical stimuli are important in host searching by *J. hunteri*. We suggest that electrophysiological studies would provide further evidence of the functions and importance of the olfactory sensilla on the *J. hunteri* antenna, as well as address their capacities to detect heat or infrared radiation, and provide additional information on the BCS sensilla described in our study.

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